With the author's compliments

Reprinted from the BOTANICAL GAZETTE, 36: 401–420, December 1903

ON THE GEOGRAPHIC DISTRIBUTION AND ECOLOGICAL RELATIONS OF THE BOG PLANT SOCIETIES OF northern NORTH AMERICA

EDGAR N. TRANSEAU
FERRY FELLOW IN BOTANY, UNIVERSITY OF MICHIGAN

PRINTED AT THE UNIVERSITY OF CHICAGO PRESS

VOLUME XXXVI NUMBER 6

BOTANICAL GAZETTE

DECEMBER, 1903

ON THE GEOGRAPHIC DISTRIBUTION AND ECOLOGICAL RELATIONS OF THE BOG PLANT SOCIETIES OF NORTHERN NORTH AMERICA.

EDGAR N. TRANSEAU.

(WITH THREE MAPS)

By the term "bog-plant societies," as used in this paper is meant that group of plant societies which is commonly found inhabiting undrained depressions and marshy grounds in the northern United States and Canada. In the northern states they have become noted for their possession of such anomalous plants as the sundew, pitcher-plant, tamarack, and cranberry. Although not so well known, the cassandra, rosemary, and Labrador tea are quite as interesting.

"DRAINED SWAMP" AND "UNDRAINED SWAMP" SOCIETIES.

There have been a number of descriptions of these bogs published in connection with local ecological studies, and in several instances have comparisons been made between them and the other swamps of the region. They are referred to as "undrained swamps," in contrast with the groups of "drained swamp" societies which may be found on adjoining low grounds and along stream courses. The latter group may be briefly summarized by noting that in the region under discussion it is commonly made up of such plants as Typha latifolia[1], Scirpus lacustris, Juncus effusus, Carex riparia, Polygonum emersum, P. sagittatum, Cephalanthus occidentalis, Cornus stolonifera, C. candidissima,

[1] Nomenclature of Britton's Manual of the Flora of the Northern States and Canada, 1901.

Salix discolor, Acer rubrum, Ulmus americana, and Fraxinus americana.

While it often happens that locally the one occurs only in drained conditions and the other only in undrained situations, field work carried on over any considerable area will show that drainage conditions are not adequate to account for the presence or absence of either of these two distinct types of vegetation. The presence of peat, with the consequent accumulation of humus acids, has been commonly spoken of as preventing the coming in of the "drained swamp" types. In southern Michigan and northern Indiana, however, there are many swamps with a thick substratum of peat and without an outlet, yet supporting a vegetation made up wholly or in part of these plants. It is true, however, that the bog societies occur here only in poorly drained situations, underlaid with peat or bogus soil.

Again, it is not unusual to find these two society groups growing on opposite sides of the same lake, where the underlying soil can be shown to be the same. To account for this, it has been suggested that the depth of water in the two situations is of importance. But any ideas of this kind can be disproved by carrying the criteria into a new locality. Just to the west of Ann Arbor, Mich., occurs a small glacial lake. This was formerly surrounded by a quite typical group of bog societies. Within recent years the eastern side of the lake has been entirely cleared, and a large part of the original tamaracks on the south and southwest sides have been cut away. There is left a rather pure growth of bog plants on the northwest side. Since the clearing was made on the southwest side there has sprung up a dense growth of herbs, shrubs, and trees, nearly equaling in height the adjoining grove of tamaracks. But if we note the species prevailing in this area, we find the plants enumerated above as typical of drained swamps. It is practically impossible to account for this situation on the basis of soil difference, chemical character of the soil solution, drainage conditions, or depth of water.

In his paper on the "Physiographic Ecology of Chicago and Vicinity" Cowles[2] distinguishes one "drained" and three

[2] BOT. GAZ. 31: 145–155.

"undrained" types of swamps occurring in the area of lakes and sand dunes at the southern end of Lake Michigan. Although several species of plants may be common to two or more, he does not believe these societies to be related to one another genetically.

That a certain amount of chance in the matter of seed dispersal must be taken into account in any botanical field problem is recognized. But the fact that "drained" and "undrained" swamps occur in close proximity to one another, each with numerous examples in the same district, seems to require some more adequate explanation.

RELATION TO SURROUNDING VEGETATION.

Throughout the region of northern Indiana, northern Ohio, and southern Michigan the problem is still further complicated by a seeming absence of all connection between the bog societies and the bordering forests. The zonal succession of plant groups, from the submerged aquatics of the pond to the arborescent forms of the higher bog margin, are clearly defined and well known. But then comes a sudden break, and without a suggestion of gradation the surrounding forest of mature oaks or oaks and hickories appears.

Farther north in Michigan there is no such difficulty in finding a definite order of succession between the bogs and forests surrounding them. For example, a tamarack swamp on north Manitou Island, which is surrounded by a thick forest of maple and beech, shows the following societies arranged almost zonally, beginning with the open pond in the center:

1. AQUATIC SOCIETY. Potamogeton natans, P. lucens, Nymphaea advena, Castalia odorata.

2. CAT-TAIL-DULICHIUM SOCIETY. Typha latifolia, Phragmites Phragmites, Menyanthes trifoliata, Dulichium arundinaceum, Cicuta bulbifera, Scheuchzeria palustris.

3. CASSANDRA SOCIETY. Chamaedaphne calyculata, Dryopteris Thelypteris, Sphagnum sp. ?, Kalmia glauca, Sarracenia purpurea, Ledum groenlandicum, Lycopus americanus, Triadenum virginicum, Polygonum Hydropiper, Rubus hispidus, Comarum palustre, Andromeda Polifolia, Chiogenes hispidula, Oxycoccus Oxycoccus, and Eriophorum virginicum.

4. SHRUB AND YOUNG TREE SOCIETY. Aronia arbutifolia, Ilicioides mucronata, Rosa caroliniana, Ilex verticillata; young specimens of Larix laricina, Betula pumila, Picea Mariana, and Acer rubrum. Beneath these occur a scattering of members of the preceding society, together with Limnorchis hyperborea, Blephariglottis lacera, Gymnandeniopsis clavellata, Osmunda regalis, O. cinnamomea, Dryopteris spinulosa intermedia, Vaccinium canadense, Epilobium lineare, E. adenocaulon, and Viola blanda.

5. CONIFER SOCIETY. This zone is composed of mature tamaracks, black spruces, low birch, and swamp maples; young and mature Betula lutea and Tsuga canadensis; and seeding Acer saccharum. The undergrowth of herbs and shrubs is diminished to a few stragglers. This brings us to the higher ground surrounding the bog, which is occupied by the next society.

6. CLIMAX FOREST SOCIETY. Consists of sugar maples and beech trees with occasional hemlocks. The undergrowth is sparse, consisting principally of their own seedlings.[3]

Going farther north into Ontario, the series of societies is not so long, but apparently just as definite. But we have there passed the northern limits of our broad-leaved mesophytic trees and the climax stage is reached in a mixed forest of pine, spruce, and fir. This same statement probably holds for the great coniferous areas of Wisconsin, Minnesota, New York, northern Pennsylvania, and the New England states. Even so far south as northern Indiana, in the sand-dune region, Cowles[4] has shown that where the surrounding vegetation consists of pines there is no doubt the same order of succession.

It appears then that where the northern conifers are dominant or make up an integral part of the forests, the ecological relations of the bog societies are clear. In other words, they normally represent one physiographic starting-point for the development of the great conifer forest formation.

There remain therefore at least two questions to be solved:

[3] See also WHITFORD, H. N., The genetic development of the forests of northern Michigan. BOT. GAZ. 31:315. 1901.

[4] *Loc. cit.*, p. 150.

First. What relation do these bog societies bear to the surrounding vegetation of oaks and hickories as they occur in Ohio, Indiana, and southern Michigan?

Second. How can we account for the presence of bog societies and swamp societies (or mixtures of the two) when found in adjacent areas, having similar drainage and soil conditions?

PRESENT DISTRIBUTION OF BOG PLANTS.

In order to obtain a better understanding of these questions, data on the geographic distribution of bog plants were collected and maps drawn. It soon became evident that the number of species would have to be limited and that only those which are characteristic of these situations across northern North America could be considered. The number was finally reduced to fifteen. Beginning with those which first find a foothold in such depressions and continuing in their approximate order of advent, they are: Menyanthes trifoliata, Dulichium arundinaceum, Comarum palustre, Scheuchzeria palustris, Eriophorum polystachyon, Drosera rotundifolia, Sarracenia purpurea, Oxycoccus Oxycoccus, Chiogenes hispidula, Andromeda Polifolia, Chamaedaphne calyculata, Ledum groenlandicum, Kalmia glauca, Betula pumila, and Larix laricina.

Finally the accompanying map (*fig. 1*) was drawn by superimposing the areas of North America in which each of these plants commonly occurs. In the course of its construction some interesting points in geographic distribution came to light. The dark area extending from the Atlantic to the Mackenzie basin represents a great center throughout which all these plants appear in most bogs. The lighter shaded areas north and south represent territory in which only a majority of the forms occur in the average bog, while in the lightest shaded portions only a minority of them are to be found.

CLIMATE OF THE OPTIMUM REGION.

The region of optimum distribution is limited by certain climatic barriers. On the southwest its limits coincide closely with those of the forests. Beyond this area the relation between rainfall and evaporation makes the conservation of water in

FIG. 1.—Map showing distribution of bog plants. (1) Drosera, Dulichium. (2) Sarracenia, Drosera, Dulichium, Eriophorum, Chiogenes, Chamaedaphne. (3) Dulichium, Menyanthes. (4) Drosera, Comarum, Menyanthes, Eriophorum, Ledum, Andromeda. (5) Drosera, Comarum, Menyanthes, Eriophorum, Oxycoccus, Andromeda, Ledum, Kalmia, Chamaedaphne. (6) Menyanthes, Oxycoccus, Ledum, Andromeda, Kalmia. The presence of a large number of shrubs in Alaska and Greenland is probably connected with their preservation there during glacial times.

depressions throughout the year impossible. On the south and southeast, while the rainfall and relative humidity are favorable, the intense insolation of the summer months seems to be the controlling factor. The northern boundary coincides with that of the northern limits of dense forests. According to Kjellman,[5] Kihlman[6] and Warming,[7] this boundary is controlled by the amount of snowfall, exposure to dry winter winds, and the length of the growing season. There does not appear to be any relation between the distribution of this group of plant societies and the "life zones" distinguished by Merriam.[8] Within the belt of optimum conditions the climate is characterized by great range of temperature, both daily and annual. As we go toward the east from the Mackenzie basin, this is modified by the increase in relative humidity. The summers are short, bright, and warm, with abundant rainfall, principally in the form of thunder showers. The winters are long, and extremely low temperatures may occur. The snowfall increases from a foot or two in the western part to several feet in Ontario and the St. Lawrence basin. In the Northwest Territories, where the tundra vegetation is dominant, the ground below a depth of a few centimeters is frozen practically throughout the year. Since air temperatures of 21° C. are common in late spring and summer, the plant roots and shoots must there withstand remarkable temperature differences. With the exception of the eastern maritime provinces and Maine, no part of this optimum area is comparable with the conditions which call forth the great bog development of northern Germany and Scandinavia. In the latter localities the bogs are not confined to depressions, but may occur in a variety of topographic situations. They may even invade established forests, and by raising the ground water level destroy the tree covering.[9]

[5] KJELLMAN, F. K., Aus dem Leben der Polarpflanzen. Leipzig. 1883.

[6] KIHLMAN, A. O., Pflanzenbiologische Studien aus Russisch-Lappland. Acta Soc. pro Fauna et Flora Fennica 6. 1890.

[7] WARMING, E., Ueber Grönlands Vegetation. Engler's Botan. Jahrbücher 10. 1888.

[8] MERRIAM, C. H., Life zones and crop zones of the United States. Bull. 10, U. S. Dept. Agric. 1898.

[9] GANONG, W. F., Raised peat bogs in the province of New Brunswick. Proc. Roy. Soc. Can. II. 3[4]: 131–163. 1897.

It is also worthy of note that in the southeastern part of this region the bog flora is increased in variety by a large number of plants whose range is more southerly than that of the typical bog plants. Among these are Vaccinum corymbosum, V. atrococcum, Rhodora canadensis, Aronia arbutifolia, and Viburnum cassinoides. Their distribution points to a northward migration from the southern Appalachians.[10]

VARIATIONS OF THE BOG FLORA IN GEOGRAPHIC RANGE.

But the map has a still greater significance. The dark area represents the region in which most of these plants attain their highest physical development. Those who have seen the magnificent groves of tamarack in the north, attaining a height of thirty meters and a bole diameter of a meter, will appreciate this fact when they compare them with the stunted groups of the larch in the bogs near the southern and northern limits.

Again, within this same belt, at least eight of the plants, the buckbean, cranberry, snowberry, rosemary, leather leaf, labrador tea, birch, and tamarack, are not confined to bog areas. They may be said to have there a wider life-range and are to be found in a variety of habitats. The tamarack, for example, is found on the hills and along most of the streams. With the black and and white spruce and pine, it makes up a large part of the forest. Here too the buckbean, leather leaf, Labrador tea, and birch occur along slow streams, and the rosemary, snowberry, and cranberry in moist ravines and rich woods.

Just as striking, perhaps, is the fact that as we go in any direction away from this optimum region, the first plants to diminish in size and frequency of occurrence are the arborescent tamarack and birch. Then follow in close succession the shrubby forms, and finally the herbaceous species.[11] This is practically a reversal of the order of their coming into a new area, and, as we shall see later on, this may have some connection with the

[10] ADAMS, C. C., Southeastern United States as a center of geographical distribution of flora and fauna. Biol. Bull. 3: 123. 1903.

[11] *Scheuchzeria palustris* is an exception, so far as its eastern distribution is concerned, and has about the same range as *Betula pumila*, but in the west it reaches its southern limit in Colorado and California.

migration this vast aggregate of bog societies has made since the glacial period. It also represents an order from the tallest forms to those raised but slightly above the wet substratum.

PREGLACIAL DISTRIBUTION.

Of these fifteen species, three, Dulichium, Sarracenia, and Kalmia, are endemic. The larch and birch are represented in the Old World by closely related forms, while the remaining ten occur in similar habitats in Europe and Asia. This naturally points to their origin, and certainly indicates their preglacial distribution to have been in the circumpolar regions of both continents. It also implies that these great land masses must have been connected for a long time during the Tertiary period, so that migration from one to the other was by no means difficult. Whether these forms originated in a single polar area is of little consequence. They may have arisen partly in America, partly in Eurasia, but they were essentially the products of similar conditions and by migration came to be associated.

THE GLACIAL MIGRATIONS.

With the coming on of the cold period, which closed the Tertiary and inaugurated such extremes of climate between the equator and the poles, the consequent accumulation of ice on these northern continents destroyed the ancient habits of these plant societies. At the same time semitropical species, which were common alike to high and low latitudes, were killed by the increasing cold, the ground they had covered affording new areas for occupancy. By the reversal of the drainage lines and consequent destruction of low-ground vegetation, new habitats suited to these plants arose in advance of the ice invasion. Just as the zones of vegetation in a small lake move toward the center, because that is the only direction in which development is possible, so these plants spread away from the centers of ice accumulation. Where this migration moved to the west the plants were later on destroyed, but their southward extension brought them into areas which were not within reach of the subsequent ice invasion. Their adaptations for rapid seed dispersal are not

notable, except in the case of the Dulichium and cottongrass. The larch and birch have winged seeds, while the remainder would seem to be dependent upon transportation by birds and water currents. But the fact that the plants have survived the ice advances proves that they were easily able to establish themselves in new areas as rapidly as the climate changed. Not less than five such geographic migrations of more or less latitude, corresponding with the five glacial epochs, must have occurred. Between them were intervals when the temperature, as shown by plant and animal remains[12] found in interglacial deposits, was fully as high as at the present time. If we consider this proved, then the only glaciation which could materially affect the distribution of our boreal societies today is that of the last or Wisconsin epoch. Through the work of Chamberlin,[13] Leverett,[14] Salisbury,[15] Upham,[16] and others, the limits of this ice invasion have been definitely mapped.

In order to get an idea of the distribution of the boreal plant societies during the maximum glaciation, let us try to picture what would become of these same societies if a similar period of glaciation were to come upon them now. A sufficient time has probably intervened since the last glacial epoch to allow of almost perfect climatic adjustment on the part of the tundra and conifer societies, so that the climate now most favorable for their development may well have characterized a zone just beyond the ice margin. This zone would gradually move with the increase of the ice fields until it would come to occupy the position shown in *fig. 2*. According to Chamberlin, the climatic conditions pre-

[12] COLEMAN, A. P., Glacial and interglacial beds near Toronto, Jour. Geol. 9: 285. 1901. PENHALLOW, D. P., The Pleistocene flora of the Don Valley. Rept. Brit. Ass. Adv. Sci. 1900: 334.

[13] CHAMBERLIN, T. C., Classification of American glacial deposits. Jour. Geol. 8: 270; The glacial phenomena of North America, Geikie's *Ice Age*, 3d ed. p. 274. 1894.

[14] LEVERETT, F., Changes of climate indicated by interglacial beds. Proc. Bost. Soc. Nat. Hist. 24: 455. 1890.—The Illinois glacial lobe. Mon. 38, U. S. G. S.—The glacial formations and drainage features of the Erie and Ohio Basins. Mon. 41, U. S. G. S.

[15] SALISBURY, R. D., and ATWOOD, W. W., The geography of the region about Devils Lake and the Dalles of the Wisconsin. Bull. 5, Wis. Geol. and Nat. Hist. Sur. SALISBURY, R. D., Glacial geology of New Jersey. Rep. State Geologist N. J. 5. 1902.

[16] UPHAM, W., The Glacial Lake Agassiz. Mon. 25. U. S. G. S. 1896.

FIG. 2. — Map showing hypothetical distribution of forests and tundra during maximum glaciation of the Wisconsin Epoch.

vailing about the margin were intermediate between those of Greenland and Alaska at the present time. In the former case the vegetation is sparse and of tundra type, in the latter the forests occur on the stagnant ice margin.[17] It would appear then that the glaciers would not affect the tree distribution at any great distance from the ice front. But there are other factors which would affect the breadth of the zone of conifer dominance. As we may learn from their present distribution, a dry climate, a youthful topography in which erosion is active, high elevation and sterile soil, all of which imply great variations in temperature and relative humidity, are more favorable to conifers than to broad-leaved deciduous trees.

It should also be noted in connection with the development of the continental glacier that, as the ice sheets spread from the two great centers of accumulation, they unite in the region north of lakes Superior and Huron. With their near approach to the lakes, the area of conifers is divided into an eastern and western section. As the development proceeds toward the Wisconsin terminal moraine, the western section would be forced toward the Great Plains, while the eastern division would spread south to the Appalachian highlands and coastal plain.

But in the interior the Ohio basin was occupied by the oaks, ash, hickories, elms and maples. Judging by the present northern limits[18] of some of these species it is doubtful if the conifers could compete with them at any great distance from the ice front, so that the belt of tundra and conifers may have extended as far south as the Ohio, but it seems probable that even north of this river species of oak, ash elm, and maple persisted.

DISTRIBUTION DURING MAXIMUM GLACIATION.

To be more definite, let us briefly note the conditions that would prevail during the time of maximum extension, from the Atlantic to the Rockies. In New Jersey, with its extensive area of sand and slow-flowing streams, conditions must have been

[17] RUSSELL, I. C., Glaciers of North America. Ginn & Co. 1901.

[18] BELL, R., The geographical distribution of forest trees in Canada. Scot. Geog. Mag. 13:281. 1897.

favorable for a wide-spreading zone of boreal societies. In Pennsylvania the high relief of the Appalachians and consequent low temperature also afforded exceptional opportunities for the spread of these societies far to the south. Here too the cold water of the glacial drainage pouring down the numerous tributaries of the Allegheny, Susquehanna, and Delaware rivers may have had a marked influence by lowering the temperatures of the narrow valleys, just as the streams which flow from Mount Katahdin and the glaciers of Mount Hood (Cowles) and Mount Shasta (Merriam)[19] affect the temperature of their adjacent valleys today. The presence of many such northern forms as the white pine, spruce, and hemlock in areas of the southern Appalachians has long been attributed to the glacial period.[20] In the Ohio valley the streams flowing from the south would aid in maintaining equable temperatures and preserving the broad-leaved mesophytes as far north as the Ohio River. Beyond the Mississippi the conditions must have resembled those now prevalent in the Saskatchewan basin. Bessey[21] reports the occurrence in Nebraska of deposits of "well defined branches, twigs and occasionally tree trunks" at depths varying from twenty to fifty feet below the surface, and concludes that in recent geological times there must have been extensive conifer forests throughout the state. The present distribution of trees in Nebraska shows outliers of the western yellow pine (*Pinus ponderosa scopulorum*) in the central part of the state far removed from the main area of its occurrenee.

Now as to the bog plants: since under favorable conditions they may occupy other habitats than undrained depressions, they probably existed on the borders of the heavily loaded streams, in ravines and moist situations generally along the whole ice front. It is to be noted that practically all of the

[19] MERRIAM, C. H., Results of a biological survey of Mt. Shasta, California. North Americana Fauna no. 16. 1899.

[20] GRAY, A., Forest geography and archaeology. Amer. Journ. Sci. and Arts III. 16:85. 1878. HOOKER, J. B., The distribution of North American flora. Amer. Nat. 13:155. 1879.

[21] BESSEY, C. E., The forests and forest trees of Nebraska. Ann. Rep. Neb. State Bd. of Agri. 1888:93.

existing small lake areas of the northern states were covered by the ice during the maximum extension of the Wisconsin ice sheet. As there is no reason to believe that the drift sheets of the preceding epochs, which in many places extend beyond the Wisconsin terminal moraine, contained such small undrained depressions, it follows that the bog societies must have occupied other habitats.

POSTGLACIAL NORTHWARD MIGRATION.

With the renewal of a milder climate and the consequent recession of the glaciers, the plant societies would gradually spread in the direction of continuous habitats and generally northward. The bog and tundra types would be the first to push into the barren ground left by the retreating ice. The area over which they spread in early postglacial times must have been very much more extensive even than that now occupied by them. In the smaller glacial depressions where absence of wave action would favor littoral vegetation, the bog plants would become firmly established. On the western and eastern sides of the glaciated area the tundra would be closely followed by the conifer forests.

In the west the spreading of the conifers to the north was followed by their gradual destruction in the southwest, due to the increase in temperature as compared with the rainfall. It is possible that the rainfall in Nebraska was never any greater than at the present time. But the decrease in transpiration accompanying decrease in temperature might account for the presence there during glacial times of trees which cannot live under present conditions. The bog plants perished with the conifers and their southwestern boundaries today correspond with that of the forest.

In the east, among the highlands, exceptional circumstances were afforded for the preservation of these northern forms. Many relicts still crowd the higher elevations as far south as western North Carolina.

But in the northern Ohio valley, with its scant conifer vegetation, the areas which at that time supported the bog societies

were encompassed by broad-leaved forests. The oaks, hickories, maples, ash, and elm, following the lines of their specific habitat, the stream valleys or uplands, the sandy stretches left by glacial drainage, or the long lines of clay moraines, surrounded them in their northward progression.

Probably if the pines, spruce, and hemlock had ever been dominant in Ohio, Indiana, and southern Michigan we should find some evidences of their former occupation by way of isolated conifer areas. Excepting the southern and eastern shore of Lake Michigan and two small groups of pines in Ingham and Calhoun counties, Michigan, no conifer areas occur south of the Grand and Huron River valleys. When the early settlers moved into the region of southern Michigan, its forests were of the type commonly known as "oak openings." Probably no type of broad-leaved forest would be more favorable for the preservation of conifer areas had they been dominant for any great length of time after the ice retreat. Where they have been planted within this region, they flourish and attain their normal proportions. Judging by the present distribution of *Pinus Strobus* and *Pinus resinosa*, the character of the soil in the vicinity of lakes Michigan, Huron, and Erie, and the meteorological conditions associated with these lakes, it seems probable that the conifers have reached their present distribution in the lower peninsula of Michigan by way of the lake shores. Probably the great bulk came by way of the southern end of Lake Michigan and from Ontario.

In the west, the north, and the east, then, the xerophytic bog societies are still found with their natural associates, the conifers (*fig. 3*). But in the Ohio valley they have been surrounded by a vegetation which bears no direct relation to them. Naturally, therefore, we should not expect to find an order of succession between them. This seems to be the answer to the first question proposed.

RELATION OF BOG SOCIETIES TO THE SWAMP SOCIETIES.

This also gives us a new basis for answering the second question, as to the presence of the bog societies and swamp societies

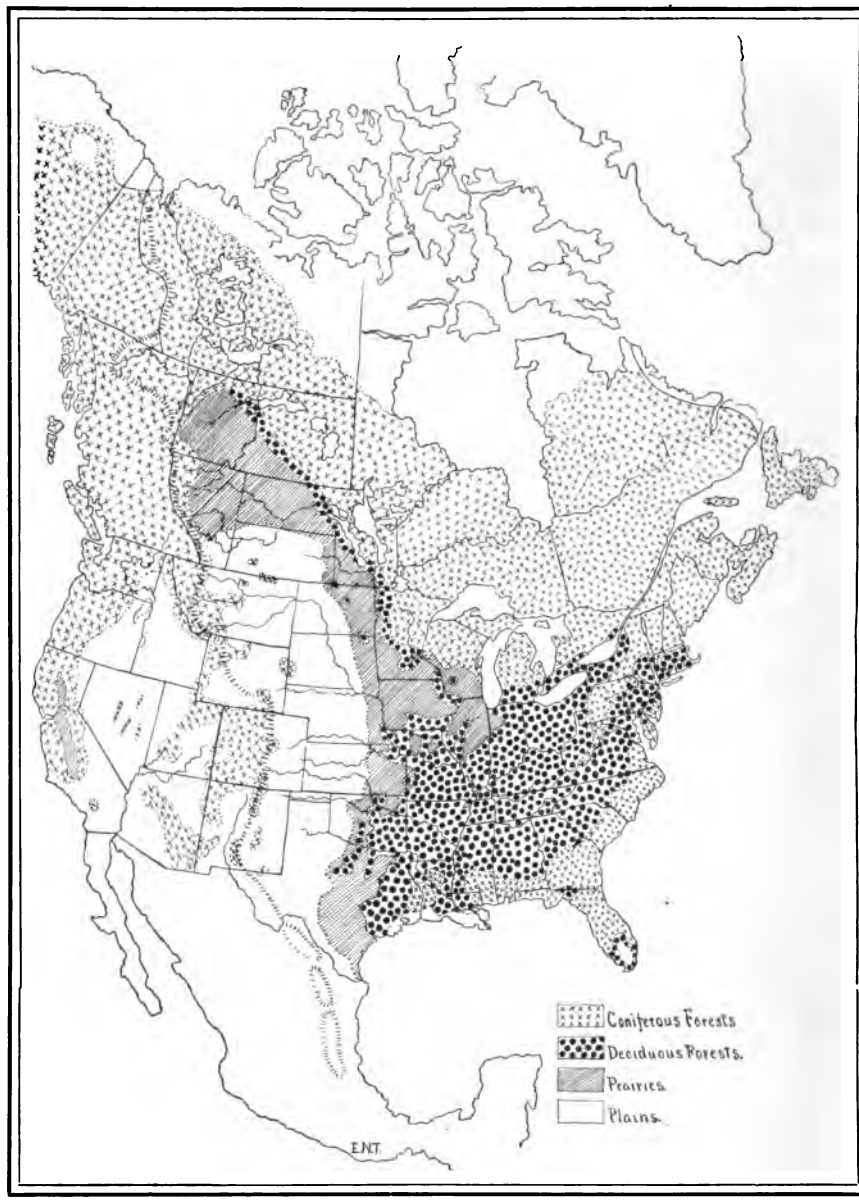

FIG. 3. — Map showing present distribution of forest, prairie and plains. (After Sargent, 10th Census, Vol. 9.)

in adjacent areas. As we know from the numerous physiographic studies that have been made of glacial basins, many of the lakes were formerly much larger than at present. Some of them in early postglacial times had steep banks, which were unfavorable to the development of shore vegetation. But by the lowering of the water level consequent upon the cutting down of the outlet, the shore line at present is a gradually sloping one, and supports a "drained swamp" flora. In other cases irregular arms, extending away from the main body of the lake and protected from wind and wave action, doubtless supported a bog vegetation during the tundra dominance. Since then they have been separated from the main lake by a lowering of the water level. Today we find in many such cases the bog vegetation still persisting in the depressions which were formerly arms of the lake, while on the shore of the main body, which came to be swampy at a much later period, the so-called "drained swamp" flora occurs. One of the best examples of this is Turkey Lake, Indiana. Here is an irregular lake several square miles in extent, nearly surrounded by high moraines. At its southeastern end, through a less elevated portion of the moraine, it formerly connected with several shallow depressions,[22] all of which contain bog plants with varying proportions of swamp plants. But on the now shallow margins of the present lake only the swamp plants are found. At Eagle Lake[23] the same observations hold for a former extension of this lake toward the northwest. But without multiplying examples, the relation of these two groups of swamp societies seems to depend largely upon the time when the swamps came into existence as swamp habitats. If they have existed since the days of tundra conditions they may show a bog flora today. If they are of recent origin, the plants will correspond to the normal swamp plants of the present climatic conditions. If of intermediate age, we may have various mixtures of the two. Dr. Cowles informs me that the only bog in the sand-dune region near Chicago which contains all these typical bog plants is the one that occurs on the Valpa-

[22] For map and description of lake see Proc. Ind. Acad. Sci. 1895.

[23] Map opposite p. 118, Proc. Ind. Acad. Sci. 1901.

raiso moraine. When this basin was formed the area occupied by the other bogs was still covered by the waters of Lake Chicago (now Michigan). At the present time new bog areas are being continually added by the interference of the moving dunes with drainage lines. And these new areas frequently contain a number of the bog plants. This, however, does not invalidate the explanation here suggested. The bog habitat has been continuous since early postglacial times; only its position and extent have been variable.

This same observation holds in the case of certain lakes which have long supported a growth of the bog plants at some part of their shore line. By recent gradual changes of level, or by the development of a floating sedge and cassandra zone, these areas have been greatly enlarged in recent times. Usually, however, such formations are partially made up of swamp species.

It is a well-known fact that in many localities where the bog societies formerly existed, they have partially or entirely disappeared. Since the settlement of this region, extensive bog areas have been cleared and drained. Fires have aided in the destruction of the tamaracks, and in many places the sudden lowering of the water level due to ditching has resulted in the killing of a large part of the original bog flora.

In this connection it is to be noted that the partial clearing or burning of a swamp area opens up a new territory for occupation, either by the bog plants or the swamp plants. The preservation of the underground stems of many of the bog species makes their chances more favorable for capturing the area in question. But there are many areas to the west of Ann Arbor which show that these bog plants cannot compete with the swamp plants in the occupancy of new territory, even though the bog plants be in complete possession previous to the clearing. We may say that the chances of capturing newly exposed land areas at the present time are all in favor of the swamp plants, largely because of their greater production of seeds, more adequate means for seed dispersal and better adaptations to present climatic conditions. In early postglacial times, however, the conditions were far different. The swamp plants had been

driven further south. The climate being more boreal in its character favored the bog plants, so that they became practically the only competitors for the low-ground situations.

The preservation of the bog societies in poorly drained situations down to the present time seems to be due (1) to the lower temperatures prevailing there, (2) to the sterile nature of the substratum, (3) to the completeness with which the substratum is occupied by the bog plants, and (4) to the fact that most bog habitats are associated with lakes, whose basins must be entirely filled with débris, before the drainage conditions will be naturally improved and made more favorable for the coming in of other plant societies.

To account for the xerophytic character of many of the bog plants, experiments now being carried on seem to indicate that differences of temperature between substratum and air is adequate. But the presence in many of our bog habitats of swamp species which show no xerophytic adaptations suggests that such xerophytic structures may be unnecessary under present conditions in *this* region.

SUMMARY.

To summarize the results of this study, we may say that, as shown by their geographic distribution:

1. The bog societies are typical of the colder portions of North America and are closely related to the bog societies of Europe and Asia.

2. They show an optimum region of dispersal having a moist climate, subject to very great temperature extremes. Within this region the plants have a greater range of habitats and an increased physical development.

3. As we go away from this center, either north or south, the first forms to show the effect of climatic change in diminished size and frequency of occurrence are the arborescent species. The species which extend furthest from this optimum region are herbaceous forms.

4. The bog societies are normally related to the conifer forests in their development to a climax tree vegetation.

5. Where surrounded by oaks and hickories, or in general

when conifers are absent, they show no order of succession to the forest societies. This is to be explained on the basis of the migrations forced upon all boreal societies during glacial times.

6. The absence of conifers in the Ohio basin probably indicates the dominance of broad-leaved forms there during glacial times.

Local lake and bog studies seem to indicate that:

1. Present bog habitats are continuations of similar habitats which existed in early postglacial times, when tundra conditions and tundra vegetation were dominant.

2. The temperature phenomena of undrained depressions, containing deposits of peat, are favorable to the preservation of these types.

3. The "drained swamp" and "undrained swamp" classification will not hold over any great area. Undrained and drained depressions are both favorable to the development of the common swamp plants.

4. The bog societies are composed of boreal species and, in so far as the area of Ohio, Indiana, and southern Michigan is concerned, must be considered as relicts of former climatic conditions. The swamp societies, made up of more southerly forms, must be considered as the normal hydrophytic vegetation of the present climatic conditions.

The above results are put forth preliminary to a more detailed account to be published later. It is hoped that by this publication the author may be enabled to secure further data as to bog societies in other localities.

UNIVERSITY OF MICHIGAN.